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# Seasonal variation in density dependence in age-specific survival of a long-distance migrant

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**Abstract.** Density dependence in vital rates is key to population regulation. Rather than being constant, the strength of density dependence may vary throughout the year, but empirical evidence is limited. Based on 22 years of data of color-banded birds from a recovering population of Eurasian Spoonbills *Platalea leucorodia leucorodia*, we show, for the first time, seasonal variation in density dependence in survival of a long-distance migrating bird. Combining resightings and dead recoveries at breeding, stopover, and nonbreeding areas enabled us to (1) separate true survival from permanent emigration from the breeding area, and (2) estimate survival in three seasons: summer, early winter (including autumn migration), and late winter (including spring migration). Accompanying the rapid population growth, juvenile annual survival initially increased, manifested in early winter, but thereafter, at high population sizes, it strongly decreased through a combination of decreasing survival in all seasons. Annual survival of subadult (second- and third-year) and adult birds decreased more gradually with increasing population size, with density dependence occurring in early winter for subadults and late winter for adults. Thus, the shape and strength of density dependence in survival varied with age and season. Understanding the seasonal timing of density dependence, especially with reference to underlying mechanisms, is important for the design of effective conservation strategies.

**Key words:** Barker model; density dependence; Eurasian Spoonbill; mark-recapture; migration; *Platalea leucorodia*; population limitation; population regulation; random effects; seasonal survival.

## INTRODUCTION

Density dependence is key to the regulation of wildlife populations (Lack 1954). Detecting density dependence has been done mostly on an annual basis, using time series analyses of population sizes (reviewed in Newton 1998, Brook and Bradshaw 2006), or correlating population size with annual reproductive output (e.g., Both 1998, Rodel et al. 2004, Armstrong et al. 2005) or annual survival (e.g., Achord et al. 2003, Armstrong et al. 2005, Owen-Smith et al. 2005, te Marvelde et al. 2009). Yet, rather than being constant, the strength of density dependence may vary throughout the year (Runge and Marra 2005, Ratikainen et al. 2008) as a result of seasonal variation in food availability (Skogland 1985, Martin 1987, Sherry et al. 2005), nutritional demands (Bryant and Tatner 1988, Doherty et al. 2001, Tinbergen and Williams 2002), disease risk (Nelson et al.

2002), or even predation risk, assuming that they act in a density-dependent manner. This may result in seasonal variation in the strength of density dependence in (especially) survival and is likely to be particularly pronounced in animals living in strongly seasonal environments and in migratory animals that visit multiple sites during the year.

Although the population consequences of seasonal variation in density dependence in survival have been investigated theoretically (Runge and Marra 2005, Ratikainen et al. 2008), notably to predict the effects of harvesting (Kokko and Lindström 1998, Boyce et al. 1999), empirical evidence of this phenomenon is limited. This is probably due to the difficulties inherent to the collection of the necessary data, as it requires long-term monitoring of populations that vary considerably in size, or studies in which population size is experimentally manipulated in all seasons (Runge and Marra 2005). The few studies that have investigated seasonal variation in density dependence in survival mainly focused on exploited species. In juvenile Atlantic salmon *Salmo salar*, density dependence in survival was strongest in autumn, the season when energetic demands were presumably highest (Bailey et al. 2010). In Willow Ptarmigan *Lagopus lagopus*, experimental harvesting

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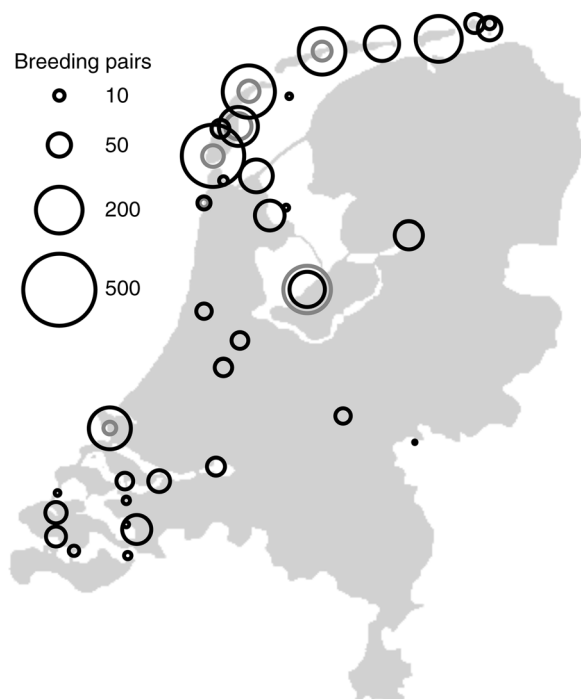


FIG. 1. Map of The Netherlands with the location and size (circle diameter indicates the number of breeding pairs) of all breeding colonies of the Eurasian Spoonbill *Platalea leucorodia leucorodia* in 1990 (gray-outlined circles) and 2010 (black-outlined circles).

regimes were compared, revealing that harvesting mortality during autumn was partially compensatory (Sandercock et al. 2011). This suggests that survival was density dependent during autumn, but in the absence of hunting in other seasons, the presence of density dependence in survival could not be evaluated for all seasons.

Here we present, for the first time, strong evidence for seasonal variation in density dependence in survival of a fully protected, non-game long-distance migrating bird. For this, we used 22 years of mark-recapture data from the Eurasian Spoonbill *Platalea leucorodia leucorodia* (see Plate 1) population that breeds in The Netherlands and has increased almost sixfold from 415 to 2338 breeding pairs during the study period (1988–2010). Combining resightings ( $n = 25\,177$ ) and recoveries ( $n = 152$ ) at the breeding, stopover, and nonbreeding areas enabled us to (1) separate annual true survival from permanent emigration from the breeding area, and (2) estimate survival in three different seasons: summer, early winter (including autumn migration), and late winter (including spring migration). We evaluate patterns of density dependence in annual and seasonal survival, while allowing for age effects (Eberhardt 2002), and discuss potential explanations for the patterns observed.

Estimates of density-dependent effects on population parameters in natural populations have, in the majority

of studies, been based on effects of natural variation in density. Strictly speaking, such analyses leave the question of causality open because the cause for the variation in density may be the same that caused the variation in the parameters studied. In continuously growing populations as discussed here, population size is also confounded with time. Yet, at this moment it is the closest we can get to model density-dependent processes as a function of age and season (or location) in a long-distance migrant.

## MATERIALS AND METHODS

### *Study population and data collection*

Our study is based on the breeding population of Eurasian Spoonbills in The Netherlands. This population is migratory and winters along the East Atlantic coast between France and Senegal (Lok et al. 2011). Due to pollution of surface waters through industrial toxic spills and insecticide use in agriculture, combined with disappearance of suitable foraging and breeding areas, the breeding population severely declined to a minimum of 148 breeding pairs in 1968 (Brouwer 1964, Koeman and van Genderen 1966). Since the prohibition of industrial toxic spilling and organochlorine pesticide use, in combination with strongly enforced protection of foraging and breeding areas (van der Hut 1992), the population has recovered to over 2300 breeding pairs in 2010, spread over 35 colonies (Figs. 1 and 2). The number of breeding pairs is accurately estimated by counting all used nests in The Netherlands during, or shortly after, the breeding season.

Between 1988 and 2010, 6482 spoonbills were color-banded just before fledging. Resightings and recoveries came from a large network of amateur and professional

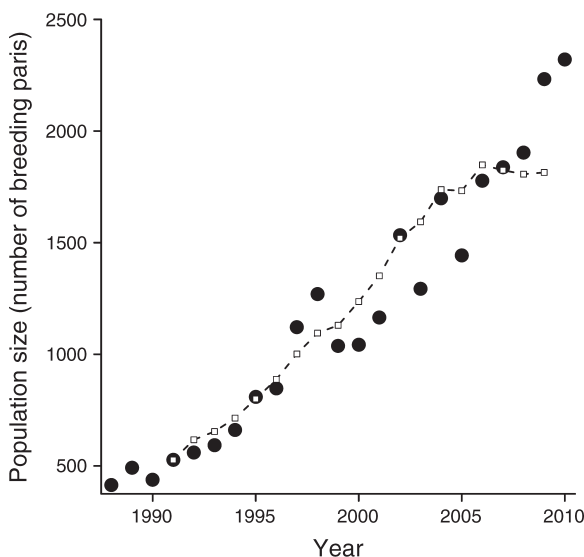


FIG. 2. Observed (black dots) and predicted (open squares) population size in terms of number of breeding pairs of Eurasian Spoonbills in The Netherlands over the years.

ornithologists in and outside The Netherlands (for details, see Appendix A: Table A1).

*Number of breeding pairs as proxy for population size*

We used the number of breeding pairs in The Netherlands to approximate the size of the population at the scale at which density-dependent processes may take place. Previous analyses showed that colony size was not a better predictor than total population size in The Netherlands for adult survival (Lok et al. 2009) or juvenile survival (T. Lok, *unpublished data*), suggesting that the main density-dependent processes did not occur locally around the breeding colonies. We did not include juvenile, subadult, and nonbreeding adult birds in our estimates of population size, because counts of these classes were generally incomplete and unreliable. However, the overall size of the population should strongly correlate with the size of the breeding population. In addition, the Dutch population mixes with other populations from Western Europe and Mauritania during the nonbreeding period. After The Netherlands, Spain harbors the largest breeding population of spoonbills, and together they account for ~80% of the Western European population (O. Overdijk, *personal communication*). The Spanish population increased from ~500 to 1500 breeding pairs in 1988–2007 (García et al. 2009). In contrast, the population of Mauritanian Spoonbills *Platalea leucorodia balsaci* resident on the Banc d'Arguin (Mauritania) (Piersma et al. 2012) has declined from ~1600 breeding pairs in 1985 to ~750 in 2007, a decrease that appears to be mainly driven by lack of reproductive output due to predation and flooding (Triplet et al. 2008). Overall, therefore, the Western Palearctic metapopulation of spoonbills has increased, although at a relatively lower rate than the Dutch population.

*Annual true survival and permanent emigration*

Annual true survival was estimated using the Barker model (Barker 1997). In contrast to conventional Cormack-Jolly-Seber (CJS) models, where mortality is confounded with permanent emigration (Lebreton et al. 1992), the Barker model combines resightings in a core study area with resightings and recoveries from the entire geographical distribution of the species to derive estimates of both true survival and (permanent) emigration away from the study area (Barker 1997). Because immature spoonbills tend to stay on the nonbreeding grounds before they start to breed when 3 years old or older (Lok et al. 2011), using the additional data from outside the breeding area increases the accuracy of survival and fidelity estimates, especially of immature birds.

The Barker model estimates the following probability parameters:  $S$ , true survival;  $F$ , fidelity to the core study ("capture") area;  $p$ , resighting during capture occasions;  $r$ , dead recovery;  $R$ , resighting during interval;  $R'$ , resighting during the interval before death; and  $F'$ ,

immigration. Because we are interested in permanent rather than temporary emigration, we fixed immigration at  $F' = 0$ . Consequently,  $F$  gives the probability of permanent emigration (Barker et al. 2004) and the probability that an animal is temporarily absent becomes a component of the (now apparent) resighting probability,  $p$ . In this study, a capture occasion is defined as the breeding season (April–July) in The Netherlands (capture area), whereas the interval includes resightings in The Netherlands during the remaining period (August–March) and resightings elsewhere throughout the year (June–May). Recoveries throughout the year are included.

The majority of spoonbills only return to The Netherlands to breed when 3 years old, although some return, but do not breed, when 1 or 2 years old (Lok et al. 2011). To account for this temporary emigration of immature birds, apparent resighting probability  $p$  in The Netherlands was modeled separately for three age classes (age 1, age 2, age  $\geq 3$ ). Annual survival was modeled separately for four age classes: first- (juvenile), second-, third-, and fourth-year or older (adult) birds. With only a single bird color-banded in 1995, age-specific survival rates could not be estimated for this cohort and were fixed to 0. Due to limited data (because only few birds return to the breeding grounds when immature), first-, second-, and third-year birds were pooled to increase the precision of the estimate of fidelity of immature birds ( $F_{012}$ ) vs. that of older birds ( $F_{\geq 3}$ ).  $F_{012}$  can be seen as an estimate of natal philopatry, i.e., the probability that a bird recruits in The Netherlands. We started with between-year variation in all (age-specific) model parameters. Adopting the notation used by Catchpole et al. (2000) and Loison et al. (2002), separate symbols were used for each age-specific parameter and parameters that varied in parallel over time were placed in parentheses (Catchpole et al. 2000, Loison et al. 2002). The fully time-dependent model was therefore written as  $S_0(t) S_1(t) S_2(t) S_{\geq 3}(t) F_{012}(t) F_{\geq 3}(t) F'(0) p_1(t) p_2(t) p_{\geq 3}(t) r(t) R(t) R'(t)$ . Optimization of this model turned out to be problematic and the simulated annealing algorithm in program MARK (White and Burnham 1999) was necessary to find the global maximum (which took three days on a fast 12-core workstation). Inspection of the parameter estimates revealed that there were many boundary estimates ( $N = 24$ ), of which 13 were among the yearly estimates of immature and adult fidelity. Because boundary estimates reflect poorly estimated parameters and may be the reason for the problematic optimization of the fully time-dependent model, we removed the between-year variation from the parameters  $F_{012}$  and  $F_{\geq 3}$  and modeled them as linear functions of population size ( $N_{\text{lin}}$ ), which resulted in a more parsimonious model (Appendix B: Table B1). Moreover, explorative analysis showed that recovery probability could be more parsimoniously modeled as constant, rather than as variable between years (Table B1). The new full model

now becomes  $S_0(t) S_1(t) S_2(t) S_{\geq 3}(t) F_{012}(N_{\text{lin}}) F_{\geq 3}(N_{\text{lin}}) F'(0) p_1(t) p_2(t) p_{\geq 3}(t) r(\cdot) R(t) R'(t)$ . This model properly converges to the global maximum using the regular optimization routine of program MARK.

Goodness of fit of this model was assessed using the median  $\hat{c}$  approach in program MARK (White and Burnham 1999). During this approach, data sets with different levels of overdispersion (extra-binomial variation) are simulated using the parameter estimates of the model of interest and then optimized with the model structure of that model. The level of overdispersion is then estimated at the value for which half of the simulated model  $\hat{c}$  are above the actual model  $\hat{c}$ . The level of overdispersion was estimated at  $\hat{c} = 1.16 \pm 0.01$  SE.

Starting from the full model, we investigated support for density dependence in age-specific survival and fidelity. For this, survival was modeled as a linear or a quadratic function of population size ( $N_{\text{lin}} = \beta_0 + \beta_1 N_t$  or  $N_{\text{quad}} = \beta_0 + \beta_1 N_t + \beta_2 N_t^2$ ) or as constant. Fidelity was only modeled as constant or as a linear function of population size, because we do not expect an initial increase in fidelity when population size is low (perhaps at the colony level, but not at the scale of The Netherlands), but only a decrease in fidelity with increasing population size. To reduce computational time and to facilitate comparison of support for the different parameterizations within a single age class, we compared the different parameterizations for each age-specific survival or fidelity parameter while modeling the other biological parameters as in the full model.

For long-term mark-recapture data sets, models with between-year variation in parameters are often preferred over constant or covariate models (Frederiksen et al. 2008). Testing the effect of covariates in such cases preferably is done while accounting for random between-year variation (Link 1999). Random-effect methodology for mark-recapture analyses has been developed by Burnham and White (2002) and has been implemented in program MARK (White and Burnham 1999). In short, the method of moments is used to separate process and sampling variation from a series of parameter estimates (in our case, yearly estimates of annual survival). Despite the suggested advantages of information-based model selection among mixed-effects mark-recapture models, we were unable to find an application for a real data set (Grosbois et al. 2008). Using the previously described random-effects methodology, we modeled age-specific survival as constant or as linear or quadratic functions of population size, while accounting for random between-year variation.

#### Seasonal survival

Seasonal apparent survival ( $\Phi$ ) and resighting probabilities ( $p$ ) were estimated using only live resightings and CJS models (Lebreton et al. 1992). Using resighting periods during the start of the summer (s1, February–May), the end of the summer (s2, July–October), and in

winter (w, December–January in Europe and October–February in West Africa), survival was estimated in three seasons: the breeding season (summer, s; April–August, 5 months), the first half of the nonbreeding season including autumn migration (early winter, w1; September–half of December, 3.5 months), and the second half of the nonbreeding season including spring migration (late winter, w2; half of December–March, 3.5 months). Because winter resightings were scarce in most years, survival during the migratory seasons could not be separated from survival in winter. Although CJS models estimate apparent survival, which is confounded with permanent emigration ( $\Phi = SF$ ), the estimates will closely resemble true survival because resightings in both breeding and wintering areas are used; i.e., birds that permanently emigrated away from The Netherlands (to breed elsewhere), as accounted for in the Barker models, can still be resighted at their wintering grounds. Moreover, whereas resightings in The Netherlands for the Barker model analysis were restricted to the core breeding period (April–July), in the seasonal survival analysis, we also included the months during which The Netherlands is used during spring and autumn migration by more northern breeding birds (February–May, July–October).

Due to the relatively low sample sizes and because of their similar behavior and annual survival (see *Results*), second- and third-year birds were pooled into one subadult age class to get more precise estimates of their seasonal survival and resighting probabilities. Birds were considered adult from the *late winter* season in their third year onward. Juvenile summer survival reflects the post-fledging period from banding (mean banding date is 11 June) until the end of August, covering  $\sim 2.5$  months.

To ensure that mortality during the migratory periods was included in the early and late winter seasons, only resightings in The Netherlands were selected for juvenile and adult birds for the summer periods. Because they stay at the nonbreeding grounds year-round, resightings of subadult birds were not restricted to The Netherlands for the summer periods. Resighting probability  $p$  was modeled as a function of age and time during the summer periods (s1 and s2) and only as a function of time during the winter period (w). Resighting probability  $p$  in period s2 was constrained to vary in parallel over time for juvenile and adult birds, because their resightings during this period are confined to The Netherlands. During the summer resighting periods, most subadult birds are resighted at their nonbreeding grounds, and summer resighting probabilities were therefore allowed to vary differently over time than those of juvenile or adult birds.

When there was substantial support for a correlation between population size and annual survival from the Barker models (see *Results*), we investigated in which of the seasons this relationship was present. This resulted in the comparison of three parameterizations for juvenile



survival (constant,  $N_{\text{lin}}$  and  $N_{\text{quad}}$ ) and two parameterizations for subadult and adult survival (constant and  $N_{\text{lin}}$ ) for each season. Because annual survival is now divided into seasonal components, there are fewer data available per season. Consequently, sampling variation was large when seasonal survival rates were allowed to vary from year to year, and many parameters were inestimable (Appendix C: Fig. C1). This resulted in covariate models being consistently preferred over between-year variation in age- and season-specific survival (Appendix C: Table C1, step 1). Because the method of moments performs poorly when sampling variation is large relative to process variation (Burnham and White 2002), we only considered fixed effects models in this seasonal survival analysis. Using similar model notation as for the Barker model, the full seasonal survival model was  $\Phi_{0,s}(N_{\text{quad}}) \Phi_{0,w1}(N_{\text{quad}}) \Phi_{0,w2}(N_{\text{quad}}) \Phi_{12,s}(N_{\text{lin}}) \Phi_{12,w1}(N_{\text{lin}}) \Phi_{12,w2}(N_{\text{lin}}) \Phi_{\geq 3,s}(N_{\text{lin}}) \Phi_{\geq 3,w1}(N_{\text{lin}}) \Phi_{\geq 3,w2}(N_{\text{lin}}) (p_{0,s2} p_{\geq 3,s2})(t) p_{12,s1}(t) p_{\geq 3,s1}(t) p_{12,s2}(t) p_w(t)$ . Using the median  $\hat{c}$  approach in program MARK (White and Burnham 1999), the level of overdispersion was estimated at  $\hat{c} = 1.61 \pm 0.003$  SE.

To reduce computational time, we proceeded in three steps. First, we checked whether resighting probability could be more parsimoniously modeled by removing age effects or between-year variation. As this substantially reduced the model fit (Appendix C: Table C1, step 2), we kept the parameterization for  $p$  as in the full model in the subsequent steps. We then investigated for each age-specific seasonal survival parameter (while keeping the other parameters as a function of population size) whether the model became less supported when the effect of population size was removed. For this, we used the criterion that when  $\text{QAIC}_c$  decreased when a parameter was removed from the model (also when less than 2 points; Arnold 2010), this parameter had a negligible effect and was removed in step 2. When removal of a parameter from the model increased  $\text{QAIC}_c$ , but by less than 2 points, the models both with and without this parameter were considered to have some support, and both parameterizations were included in step 2. When  $\text{QAIC}_c$  increased more than 2 points, the parameter was considered to have a substantial effect and was always included in step 2. In the third step, all combinations of parameterizations that were supported in the second step were compared.

#### Statistical analysis

We used program R (version 2.13.0; R Development Core Team 2011) and the package RMark (Laake 2011) to construct mark-recapture models for running in program MARK (White and Burnham 1999). To build the random-effects models, we followed the approach described by Burnham and White (2002), implemented in program MARK. In short, the method of moments is used to derive shrunken estimates at which the fixed-effects likelihood is then evaluated. This gives the

likelihood of the random-effects model. The number of parameters associated with the random-effects model can be calculated as  $K_{\text{re}} = \text{tr}(G) + \ell$ , where  $\text{tr}(G)$  is the dimension of parameter space associated with the random component of the model, and  $\ell$  is the number of remaining parameters (fixed effects) to be estimated. The random-effects models were fitted on a probability scale because boundary parameters will inflate sampling and process variation when estimated on a logit scale (Burnham and White 2002). All other probability parameters (fixed effects) were estimated on a logit scale.

To check that all Barker models had converged to the global maximum (likelihood), models were rerun using different initial values. Some reduced models (only three) turned out not to have converged properly (the estimated deviance varied depending on the initial values used), and the global maximum of these models was verified using simulated annealing. Shrunken estimates were imported into R to enable time-efficient parallel running of the random-effects Barker models on a 12-core workstation. Model selection was based on the Akaike information criterion, corrected for small sample size and overdispersion ( $\text{QAIC}_c$ ; Burnham and Anderson 2002). Reported standard errors and confidence intervals are also adjusted for overdispersion.

## RESULTS

### Annual true survival and permanent emigration

Model selection results of the fixed- and random-effects Barker models are shown in Appendix B: Table B2. Annual survival and fidelity of all age classes were best described as a function of population size (Table B2; parameterizations in bold), with random between-year variation in first-, second-, and third-year survival, but not in adult survival. First-year annual survival was best described by a quadratic function of population size, whereas annual survival of second-year, third-year, and adult birds was best described by a linear function of population size (Appendix B: Table B2). On average, survival increased from the first to the third year, but was somewhat lower in adult birds (Table 1). The decrease in survival with population size was strongest for juveniles, although only at high population sizes, and was weakest for third-year and adult birds (Fig. 3, Table 1). Fidelity of immature birds was lower and decreased more strongly with population size (from  $0.94 \pm 0.008$  (mean  $\pm$  SE) in 1988 to  $0.87 \pm 0.012$  in 2008) than that of adult birds (from  $0.99 \pm 0.004$  to  $0.95 \pm 0.010$ ). Shrunken estimates of survival and maximum-likelihood estimates of fidelity, resighting, and recovery probabilities are shown in Appendix B: Tables B3 and B4.

### Seasonal survival

The seasonal differences in survival varied with age. On average, juvenile survival (reported as  $\text{year}^{-1}$ ) was lowest in early winter ( $0.33 \pm 0.03$ ), higher in late winter ( $0.58 \pm 0.05$ ), and highest in summer ( $0.71 \pm 0.02$ ). Similarly, subadult survival was lowest in early winter

TABLE 1. Estimates of parameters, process variation ( $\sigma^2$ ), and residual variation ( $\sigma_{\text{res}}^2$ ) of the intercept ( $\mu$ ), and best-supported density-dependence random-effects mark-recapture model, by age, for annual true survival of Eurasian Spoonbills.

| Annual survival         | Intercept model |                  | Best-supported density-dependence model |                   |                   |                               | $R^2$ | $\Delta\text{QAIC}_c$ |
|-------------------------|-----------------|------------------|---|-------------------|-------------------|-------------------------------|-------|-----------------------|
|                         | $\hat{\mu}$     | $\hat{\sigma}^2$ | $\hat{\beta}_0$                         | $\hat{\beta}_1$   | $\hat{\beta}_2$   | $\hat{\sigma}_{\text{res}}^2$ |       |                       |
| First year              | $0.56 \pm 0.03$ | 0.012            | $0.67 \pm 0.02$                         | $-0.036 \pm 0.02$ | $-0.165 \pm 0.02$ | 0.003                         | 0.77  | -3.20                 |
| Second year             | $0.92 \pm 0.01$ | 0.003            | $0.91 \pm 0.01$                         | $-0.046 \pm 0.02$ |                   | 0.002                         | 0.40  | -1.34                 |
| Third year              | $0.95 \pm 0.01$ | 0.001            | $0.95 \pm 0.01$                         | $-0.032 \pm 0.01$ |                   | 0.001                         | 0.40  | -1.44                 |
| Adult ( $\geq 4$ years) | $0.88 \pm 0.01$ | 0.001            | $0.89 \pm 0.01$                         | $-0.039 \pm 0.01$ |                   | 0.0006                        | 0.51  | -1.42†                |

Notes: Population size may have a linear ( $N_{\text{lin}}$ ) or quadratic ( $N_{\text{quad}}$ ) effect:  $N_{\text{lin}} = \beta_0 + \beta_1 N_z$  and  $N_{\text{quad}} = \beta_0 + \beta_1 N_z + \beta_2 N_z^2$ , where  $N_z = (N - \bar{N})/\text{SD}$ , with  $N$  being the number of breeding pairs,  $\bar{N} = 1175$ , and  $\text{SD} = 585$ . We used  $N_z$ , the standardized population size, to speed computation; it should be used to obtain the actual true survival rate, using the beta estimates in this table. Estimates are given as mean  $\pm$  SE. The percentage of variation explained by the density-dependence model, as compared to the intercept model ( $R^2$ ), is calculated as  $1 - \sigma_{\text{res}}^2/\sigma^2$  (Loison et al. 2002).  $\Delta\text{QAIC}_c$  is calculated as  $\text{QAIC}_c$  (best-supported random-effects covariate model) minus  $\text{QAIC}_c$  (random-effects intercept model). For an overview of all the fixed- and random-effects models compared, see Appendix B: Table B2.

† Note that survival of birds  $\geq 4$  years old was by far best described by the fixed-effects  $N_{\text{lin}}$  model (see Appendix B: Table B2).

( $0.79 \pm 0.04$ ), higher in late winter ( $0.85 \pm 0.07$ ), and approached unity in summer ( $1.00 \pm 0.00$ ). Adult survival was lowest in late winter ( $0.68 \pm 0.03$ ), higher in early winter ( $0.89 \pm 0.03$ ), and also approached unity in summer ( $1.00 \pm 0.00$ ).

The effect of population size on seasonal survival also varied with age (Fig. 4). Model selection results are shown in Table C1. There was substantial support for an

effect of population size ( $\Delta\text{QAIC}_c > 4$  when the effect was removed) on juvenile survival during the post-fledging period and early winter, on subadult survival during early winter, and on adult survival during late winter. Juvenile survival decreased with population size during the post-fledging period, with the quadratic and linear effect having similar support ( $\Delta\text{QAIC}_c = 0.24$  when removing the quadratic term), whereas the

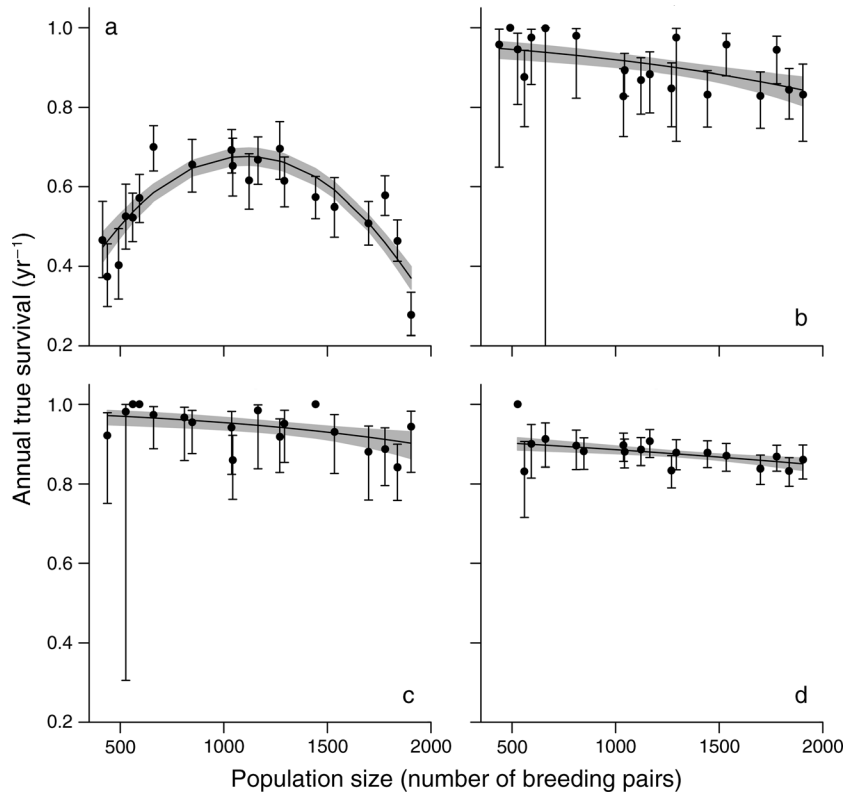


FIG. 3. Estimates of annual true survival of (a) first-year, (b) second-year, (c) third-year, and (d) adult (fourth-year or older) birds in relation to population size. The black dots represent the yearly estimates from the full model. The lines represent the estimates of the best-supported fixed-effects model per age class (see Appendix B: Table B2). Error bars and gray areas represent 95% confidence intervals for estimates from different models adjusted for overdispersion ( $\hat{c} = 1.16$ , program MARK [White and Burnham 1999] measure of the model goodness of fit; see *Materials and methods*).

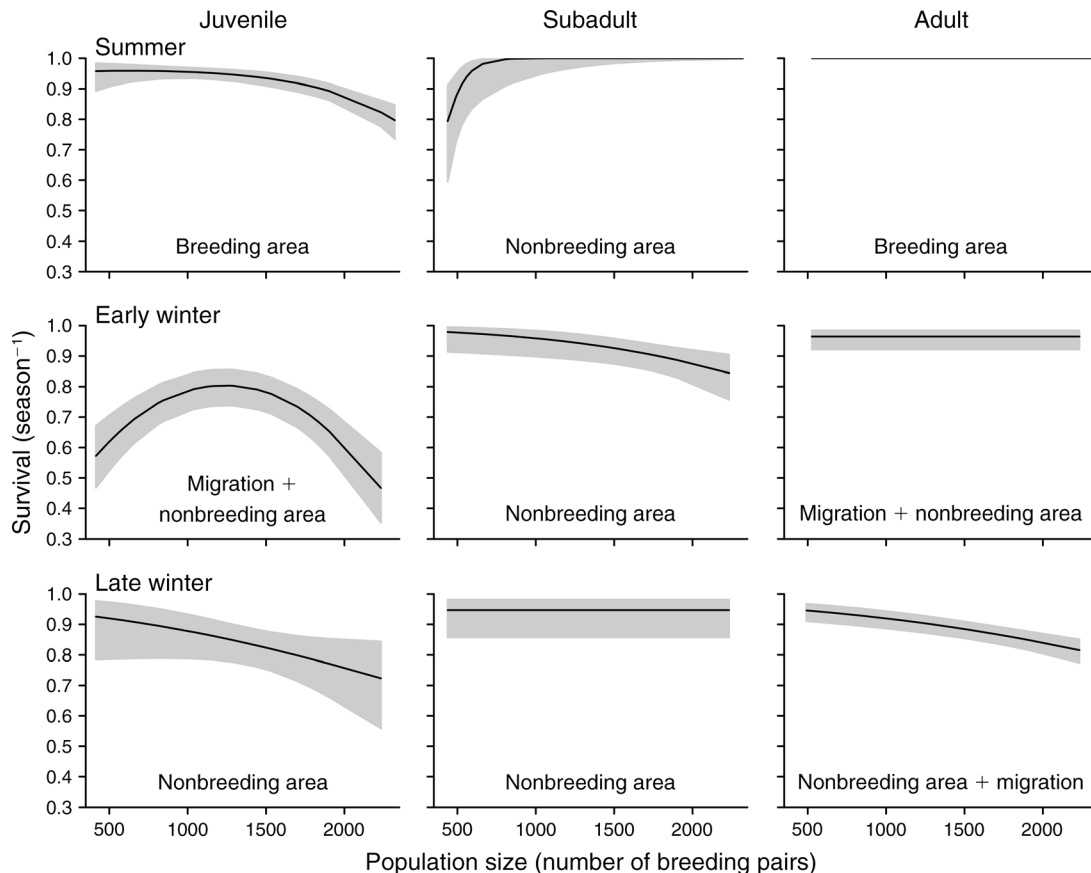


FIG. 4. Estimates (solid lines) of the relationship between population size and seasonal survival of juvenile, subadult (second- and third-year birds combined) and adult birds from the best-supported model (Appendix C: Table C1, model 29). Gray areas represent 95% confidence intervals adjusted for overdispersion ( $\hat{c} = 1.61$ ; see *Materials and methods*).

quadratic effect was clearly supported during early winter ( $\Delta\text{QAIC}_c = 3.47$ ): after an initial increase, early winter survival of juveniles decreased at high population sizes. Subadult and adult survival decreased with population size, respectively, in early and late winter. There was some support for an initial increase with population size in subadult survival in summer ( $\Delta\text{QAIC}_c = 2.40$  when the effect was removed) and for a decrease in juvenile survival during late winter ( $\Delta\text{QAIC}_c = 1.19$ ). Estimates of season- and age-specific resighting probabilities from the best-supported model (Appendix C: Table C1, model 14) are presented in Appendix C: Fig. C2. Age-specific annual survival, when calculated from the seasonal survival estimates, was very similar to the annual true survival estimates from the Barker model (Fig. C3).

#### DISCUSSION

Survival was correlated with population size, with the shape of the relationship varying among age classes and seasons. Juvenile annual survival initially increased with growth of the population, but then decreased with further population growth. Annual survival of older

birds decreased with population size throughout the study period. The initial positive effect of population size on juvenile survival was manifested in early winter, whereas at high population sizes, juvenile survival decreased with population size in all seasons. Subadult and adult survival decreased with population size in early and late winter, respectively.

To investigate seasonal density dependence in survival in the absence of accurate counts of population size in winter, we related survival in each season to the preceding number of breeding pairs in The Netherlands. By doing so, we did not account for seasonal changes in abundance due to mortality. For example, after a season of high mortality (whether or not density dependent), population size is reduced, and density dependence in a subsequent season may be relaxed (Ratikainen et al. 2008). Using the estimates of seasonal survival allowed us to estimate the seasonal changes in abundance in a post hoc fashion and adjust the interpretation of the results where needed. In our case, because juvenile survival was especially low in early winter, the number of juveniles in late winter was reduced, and consequently, the strength of density dependence in the late winter



season was underestimated to some extent. Because adult survival was lowest in late winter, the largest reduction in the number of adult birds occurred between winter and summer, which is accounted for by evaluating the adult population size in summer (by counting the number of breeding pairs). Because subadult survival was high and similar in all seasons, the number of subadult birds decreased slowly and gradually over the year.

Permanent emigration increased with population size, potentially as an escape from increased competition (for food or space) during the breeding season in The Netherlands, consistent with the northward expansion to Germany and Denmark (O. Overdijk, *personal observation*). Permanent emigration has especially increased for immature birds (Fig. 3), suggesting that natal dispersal has been more important than breeding dispersal as a mechanism of this range expansion. The estimated age-specific survival and emigration rates (Appendix B: Table B3), together with an assumed constant reproductive output ( $f = 0.62$ ; see Appendix D for calculations), resulted in a reasonable fit between predicted and observed number of breeding pairs in The Netherlands until 2008 (Fig. 2). This suggests that reproductive output is not (yet) density dependent at the scale of The Netherlands, at least not at the level that would have a pronounced effect on population growth rates. As Lok et al. (2009) found that reproductive output was strongly density dependent at the level of a single colony, the apparent absence of density dependence in reproductive output at the scale of The Netherlands suggests that the range expansion of spoonbills has coincided with the discovery of new suitable breeding habitats (Fig. 1). In fact, the deviation between observed and predicted population growth from 2008 to 2009 could have been caused partly by some preceding years with exceptionally high reproductive output. In addition, the fact that fidelity was forced to be a linear function of population size may have resulted in an overestimation of the proportion of birds that permanently emigrated during recent years of high population sizes.

At present, we can only speculate about the mechanisms underlying the relationships between population size and age-specific survival rates. We cannot exclude the potential role of density-independent factors that changed with time and thus covaried with population size over the study period. For example, many migratory bird populations have declined during the last decades; this has been correlated with climate change (Newton 2004) and (human-induced) habitat alterations (Kraan et al. 2009). However, because the season of the strongest effect of population size differs among age classes, it is unlikely that the declining survival rates are primarily caused by density-independent changes in the environment in any particular season. We now will elaborate on potential reasons for the most pronounced patterns of density dependence in seasonal survival.

#### *Age effects on strength and seasonal timing of density dependence*

Juvenile survival initially increased steeply with population size, but showed a sharp decrease at higher population sizes. The positive effect of population size on survival at low population sizes was only apparent in juveniles, not in older birds (Fig. 3). Earlier studies on Mediterranean Gulls *Larus melanocephalus* and Dalmatian Pelicans *Pelicanus crispus*, both colonial breeders as well, also found evidence of inverse density dependence in juvenile annual survival, but not in adult survival (te Marvelde et al. 2009, Doxa et al. 2010). In colonial breeders, inverse density dependence in juvenile survival might occur during the rearing period when the presence of conspecifics reduces predation risk and thermoregulatory costs (Courchamp et al. 1999, Doxa et al. 2010). We show, however, that the initial increase in juvenile survival occurs in early winter rather than during the post-fledging period (Fig. 4). Possibly, this increase in early winter survival resulted from carryover effects from positively density-dependent effects during the post-fledging period (Lindström 1999, Harrison et al. 2011). Alternatively, the presence of conspecifics is particularly important for juveniles in early winter. Because spoonbills migrate in groups consisting of both juvenile and adult birds, the inexperienced juveniles may benefit from social information for navigation and stopover site use during their first autumn migration (Henningson and Karlsson 2009). Moreover, spoonbills may use V-formation flight during migration so that the presence of others may reduce flight costs during migration (Cutts and Speakman 1994). However, this would also benefit adult birds where inverse density dependence in survival did not occur.

After the initial increase, the subsequent decrease in juvenile annual survival with population size was much stronger than in older birds, decreasing from  $\sim 0.70$  to  $0.50$  between 2000 and 2008. Stronger density dependence in juvenile than in adult annual survival was also confirmed by other studies (Fowler 1987, Arcese et al. 1992, Gaillard et al. 1998, Armstrong et al. 2005, Bailey et al. 2010). Here we show that survival of juveniles, occurring together with adults in summer and early winter, was density dependent in those seasons, whereas adult survival was not (Fig. 4). This may be explained mechanistically by food availability having declined most strongly for juveniles because they are competitively inferior (Townshend 1985, Sandell and Smith 1991), or because they are less efficient foragers (Groves 1978). Although juvenile and adult survival appeared similarly density dependent in the late winter season, this comparison is not very meaningful because juveniles stay at the nonbreeding grounds, whereas adults migrate back to their breeding grounds and prepare for breeding. Because population growth rate is generally more sensitive to changes in adult survival than immature survival (Sæther and Bakke 2000), the stronger density dependence in juvenile compared to



PLATE 1. A breeding colony of Eurasian Spoonbills on the island of Schiermonnikoog, The Netherlands (April 2006). Photo credit: T. Lok.

adult survival (although only at high population sizes) is in accordance with the commonly observed pattern that the strength of density dependence in demographic parameters decreases with increasing sensitivity of population growth rate to changes in a demographic parameter (Eberhardt 2002). That density dependence in subadult survival was not (much) stronger than in adult survival may be explained by the higher energy and nutritional demands of adult birds that migrate and breed, compared to subadult birds that generally remain on their nonbreeding grounds year-round.

*Potential mechanisms of seasonal density dependence in adult survival*

Adult survival was independent of population size in summer and early winter but decreased with population size in late winter. The strong decline in adult survival in late winter may find its cause on the wintering grounds or during spring migration. This decline may be caused by food limitation, and may be density dependent when per capita food availability is a function of population density. Sillett and Holmes (2002) have argued that during migration periods density-independent factors, such as adverse weather conditions and collisions, will be more important than density-dependent factors in causing mortality. Although this may be true for migratory passerines, density-dependent factors during migration could be important for migratory species that congregate at a limited number of staging sites, such as waterfowl and shorebirds (Newton 2006). Negative density dependence at staging sites in such cases could be strong, as bird densities are often high and resources become heavily depleted (Newton 2006). Annual survival of White Storks *Ciconia ciconia* was strongly correlated with primary production indexed by the normalized difference vegetation index (NDVI) at a

major staging area (Schaub et al. 2005). The absence of density dependence in adult survival in early winter indicates that, at least during southward migration, resource availability at staging sites is not (yet) limiting for spoonbills.

Instead of, or in addition to, food limitation at staging areas, food may be limiting on the wintering grounds. This may be due either to lower per capita food availability or to higher energy demands in winter, for example due to higher costs of thermoregulation (Wiersma and Piersma 1994, Doherty et al. 2001). This may have led to increased mortality at the wintering grounds or, via carryover effects, to increased mortality during spring migration. Many studies found a relationship between food conditions on the wintering grounds and annual survival (Peach et al. 1991, Gill et al. 2001), timing of arrival at breeding grounds, and/or reproductive output (reviewed in Harrison et al. 2011). The fact that annual survival of the subadult birds that generally remain on the wintering grounds year-round also decreased with population size (although in early rather than late winter, perhaps because subadult birds face different constraints than adult birds) suggests that at least part of the observed decline in adult survival in late winter is mediated by conditions at the wintering grounds rather than at stopover sites during northward migration. Two adult spoonbills equipped with GPS satellite transmitters died shortly after northward departure from their West African wintering grounds. Unfortunately, these birds could not be retrieved and therefore the potential role of starvation in causing death could not be assessed.

*Seasonal variation in survival*

Most mortality occurred away from the breeding grounds, although the exact timing (early or late winter)

differed among age classes. That survival in summer is highest, as compared to other seasons, is in agreement with the few other studies that investigated seasonal survival. Sillett and Holmes (2002) found that most (>85%) of the mortality occurred during the migratory seasons in a migratory passerine, the Black-throated Blue Warbler *Dendroica caerulescens*, although they compared different populations to get estimates of winter and summer survival. In the migratory Blue Petrel *Halobaena caerulea*, around 70% of the annual mortality of adult birds occurred during the nonbreeding period (Barbraud and Weimerskirch 2003). Leyrer et al. (*in press*) found that in Red Knots *Canutus canutus* using the same flyway and wintering areas as the Eurasian Spoonbills studied here, virtually all mortality occurred on the wintering grounds in West Africa. Gauthier et al. (2001) could not find seasonal differences in survival in Greater Snow Geese *Chen caerulescens atlantica*, but because they used a different categorization of seasons, the results are difficult to compare.

#### *Toward a general ecology of seasonal demography*

Generally, it can be concluded that the shape and strength of density dependence in survival varies with season and age. Determining the seasons in which survival is density dependent can now be the basis for more detailed studies on the density-dependent processes occurring in those seasons. Revealing whether density-dependent survival in any season is mediated by intraspecific competition for food and space is important to predict the effect of habitat loss in any season on migratory populations (Sutherland 1996).

Another line of investigation could focus on comparisons of demographic patterns in different species using the same flyway (e.g., the Red Knots previously discussed; Leyrer et al., *in press*) or distinct populations of the same species using different flyways (Piersma 2007). Such demographic comparisons among populations and species will increase our understanding about the generalities and specificities of the limitation and regulation of migratory bird populations.

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## SUPPLEMENTAL MATERIAL

### Appendix A

Overview of number of Eurasian Spoonbills ringed, resighted, and recovered ([Ecological Archives E094-217-A1](#)).

### Appendix B

Annual survival: model selection results, shrunken estimates of true survival, and maximum-likelihood estimates of other parameters of the full Barker model ([Ecological Archives E094-217-A2](#)).

### Appendix C

Seasonal survival: model selection results, estimates of between-year variation in seasonal survival, and resighting probabilities ([Ecological Archives E094-217-A3](#)).

### Appendix D

Population matrix model to predict population growth ([Ecological Archives E094-217-A4](#)).